# Biomass, productivity, and nutrient-use efficiency of aboveground vegetation in four Rocky Mountain coniferous forests

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Aboveground biomass, annual production, and internal nitrogen and phosphorus dynamics of vegetation were compared among a 90-year-old *Pinus contorta* Loudon forest, a 120-year-old *Picea glauca* (Moench) Voss – *P. contorta* forest, a 350-year-old *Picea engelmannii* Parry ex Engelm. – *Abies lasiocarpa* (Hook.) Nutt. forest, and a 13-year-old *P. contorta* stand in the Rocky Mountains of southwestern Alberta. Aboveground biomass of vegetation ranged from 109 to 203 $t \cdot ha^{-1}$, while aboveground net primary productivity ranged from 4.4 to 5.3 $t \cdot ha^{-1} \cdot year^{-1}$ in the mature forests. Approximately 30% of the N and 20–40% of the P in ground vegetation were reabsorbed during senescence; 40–50% of the N and 50–80% of the P were reabsorbed from senescing tree foliage. Annual uptake of nutrients (production minus reabsorption) was between 1.8 and 2.2 $g \cdot m^{-2} \cdot year^{-1}$ for N and 0.2–0.4 $g \cdot m^{-2} \cdot year^{-1}$ for P. Efficiency of nutrient use (milligrams of new biomass produced per milligram of nutrient taken up in 1 year) ranged from 249 to 262 for N and 1604 to 2355 for P in the mature forests, and 72 and 642, respectively, in the young pine stand. Both N and P were used very efficiently in the pine forest and relatively inefficiently in the spruce–pine forest, reflecting differences in the inherent nutrient-use efficiency of these tree species. In the spruce–fir forest, N was used less efficiently and P more efficiently than in other forests, in response to lower phosphorus availability in this forest. Differences in nutrient-use efficiency of vegetation were related to differences in the amount of biomass produced per unit amount of N or P taken up, and not to differences in efficiency of N or P reabsorption.

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La biomasse au-dessus du sol, la production annuelle ainsi que la dynamique interne de l'azote et du phosphore de la végétation ont été comparés dans une forêt de *Pinus contorta* Loudon âgée de 90 ans, une forêt de *Picea glauca* (Moench) Voss et de *P. contorta* âgée de 120 ans, une forêt de *Picea engelmannii* Parry ex Engelm. et de *Abies lasiocarpa* âgée de 350 ans et un peuplement de *P. contorta* âgé de 13 ans localisés dans les montagnes Rocheuses du sud-ouest de l'Alberta. La biomasse au-dessus du sol de la végétation variait de 109 à 203 $t \cdot ha^{-1}$, alors que la productivité primaire nette au-dessus du sol variait de 4,4 à 5,3 $t \cdot ha^{-1} \cdot an^{-1}$ dans les forêts mûres. Environ 30% de N et 20–40% de P dans la végétation du sous-bois ont été réabsorbés durant la phase de sénilité; 40–50% de N et 50–80% de P ont été réabsorbés à partir du feuillage des arbres vieillissants. Le prélèvement annuel des éléments nutritifs (la production moins la réabsorption) était entre 1,8 et 2,2 $g \cdot m^{-2} \cdot an^{-1}$ pour N et entre 0,2 et 0,4 $g \cdot m^{-2} \cdot an^{-1}$ pour P. L'efficacité de l'utilisation des éléments nutritifs (en milligrammes de nouvelle biomasse produite par milligramme d'éléments nutritifs prélevés en 1 année) a varié de 249 à 262 pour N et de 1604 à 2355 pour P dans les forêts mûres, et de 72 à 642 dans le jeune peuplement de pins, respectivement. Tant N que P ont été utilisés efficacement dans le peuplement de pins, et plutôt inefficacement dans la forêt d'épinettes et de pins, ce qui traduit des différences dans l'efficacité inhérente de l'utilisation des éléments nutritifs par ces essences. Dans la forêt de sapins–épinettes, N a été utilisé moins efficacement et P l'a été plus que dans les autres types de forêts, en réponse à une disponibilité plus faible du phosphore dans ce type de forêt. Les différences dans l'efficacité de l'utilisation des éléments nutritifs de la végétation étaient reliées aux différences observées dans les quantités de biomasse produites par quantité de N ou P prélevées, et non pas aux différences dans l'efficacité de la réabsorption de N ou P.

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## Introduction

Quantification of the internal nutrient dynamics of vegetation is an essential component of studies of nutrient cycling in terrestrial ecosystems. Measurement of the mass and nutrient concentrations of vegetation provides information on the mass of nutrients immobilized in plant biomass and amounts required for annual production. It also allows determination of nutrient-use efficiency (NUE) of vegetation, which may be indicative of levels of available nutrients in soil (Vitousek 1982; Pastor *et al.* 1984; Shaver and Melillo 1984). Vegetation on infertile sites tends to use nutrients more efficiently than vegetation on fertile sites, as a consequence of replacement by more nutrient-efficient species (Small 1972; Chapin and Kedrowski 1983) or increased efficiency of persistent species on nutrient-poor sites (Boerner 1984; Kost and Boerner 1985). More efficient use of nutrients may arise through greater biomass production per unit of nutrient uptake (Birk and Vitousek 1986; Lajtha and Klein 1988), or in perennial plants, through greater reabsorption of nutrients from senescing tissues (Stachurski and Zimka 1975; Turner 1977; cf. Chapin and Kedrowski 1983). NUE may be determined from annual estimates of mass of nutrients immobilized in, and reabsorbed from, foliage, or inferred from nutrient concentrations in foliage and litter.

The present investigation is part of a larger study comparing cycling of nitrogen and phosphorus in four distinct

TABLE 1. Characteristics of the forests at the four study sites in the Rocky Mountains of southwestern Alberta

| Site | Elevation (m) | Slope (deg.) | Aspect | Age[a] (yr) | Density[b] (stems/ha) | Basal area[b] ($m^2 \cdot ha^{-1}$) | Forest floor depth[c] (cm) |
|---|---|---|---|---|---|---|---|
| Clearcut | 1410 | 0 | — | 13 | 0 | 0 | 3.9 ± 0.8 |
| Pine | 1530 | 0 | — | 90 | 1716 | 30.52 | 6.4 ± 1.4 |
| Spruce | 1500 | 3 | NW | 120 | 750 | 39.14 | 11.9 ± 3.9 |
| Fir | 1830 | 30 | WNW | 350 | 1177 | 40.04 | 12.1 ± 4.2 |

[a]Apparent age since last fire, or time since cutting at the clearcut site.
[b]Values for canopy trees only; >10 cm DBH for subalpine fir, spruce, and aspen; >5 cm DBH for Douglas-fir, pine, and poplar.
[c]Values are given as mean ± standard deviation of 40 samples.

coniferous forests within a single watershed. The purpose of this paper is to characterize the aboveground vegetation in each forest according to composition, biomass, and productivity, and to compare the efficiency with which N and P are used by the vegetation in each forest.

## Study area

The forests chosen for study were in the front range of the Rocky Mountains in the Kananaskis Valley of southwestern Alberta, Canada (51°2′N, 115°3′W). This area was last glaciated 20 000 years ago. Most of the study area is located within the Montane ecoregion of Alberta (Strong and Leggat 1981). This region is subject to both Prairie and Cordilleran climatic influences. Mean monthly temperatures at the Kananaskis Centre for Environmental Research, located in the study area, range from −10.2°C in January to 14.1°C in July. The frost-free period averages 58 days, from 24 June to 22 August. Mean annual precipitation is 657 mm, of which 292 mm occurs as snow. Peak precipitation occurs in June. Snow cover is discontinuous because of frequent warm chinook winds throughout the winter. Variations in this climatic regime occur at different aspects and elevations. South- and west-facing slopes are usually warmer and drier than north- and east-facing slopes (Karkanis 1972), and increasing elevation is associated with cooler temperatures and greater winter precipitation.

Vegetation in the Kananaskis Valley is composed of a lower montane zone of lodgepole pine (*Pinus contorta* Loudon) and white spruce (*Picea glauca* (Moench) Voss) or white × Engelmann spruce hybrids, and an upper subalpine zone of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) or white × Engelmann spruce hybrids, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Fire is the major type of disturbance influencing forests in the valley; stand-replacing fires occur every 100 years on average (Johnson 1987).[1] Lodgepole pine regenerates most rapidly after a severe fire, often forming dense even-aged stands (Day 1972; Wheeler and Critchfield 1985). Spruce may also regenerate after fire, given an adequate seed source and sufficient moisture (Alexander 1987). Trembling aspen (*Populus tremuloides* Michx.) regenerates rapidly via suckering after less severe fires (Parker and Parker 1983). After canopy closure, spruce and fir become dominant in the understory. Given a sufficient period of time between fires, as occurs at higher elevations, spruce and fir come to dominate the overstory. Different life-history traits of spruce (long life-span, low recruitment) and fir (short life-span, high recruitment) allow both species to remain in old-growth forests (Veblen 1986; Aplet *et al.* 1988). Additional information on the physical environment is available in the Kananaskis Country Environmental Education Library (Kananaskis Country Environmental Education Coordinator, Canmore, Alberta). Nomenclature of plants follows Moss (1983).

[1]E.A. Johnson. 1987. Fire frequency in the Kananaskis River watershed. Final Report to Alberta Environmental Research Trust, Calgary, Alberta.

## Site description

Within this mosaic of forests in the Kananaskis Valley, four stands of distinctly different overstory tree composition were selected for study. All stands were within 5 km of one another in the Lusk Creek watershed (51°02′N, 115°03′W). Soils in the watershed are mostly well-drained brunisols of sandy loam texture derived from predominantly limestone parent material. Glacial reworking of parent material has led to intermixing of calcareous and noncalcareous rocks in the watershed (Crossley 1951). Study sites were named according to the dominant species of overstory tree in the stand, pine, spruce and fir, and the fourth was a clearcut; they are described in Table 1.

The pine site was located on a flat ground moraine of glacial till (Stalker 1973) at 1530 m elevation. The soil was an Orthic Eutric Brunisol. Canopy trees were almost exclusively lodgepole pine 70–90 years of age and 15 m in height. Density of canopy trees was 1716 stems/ha; stand basal area was 30.5 $m^2$/ha. Extensive natural thinning had already occurred in this stand, with considerable numbers of standing dead and fallen pines, all of DBH <10 cm. Spruce, poplar (*Populus balsamifera* L.), and aspen dominated the understory. The shrub layer was composed of buffalo-berry (*Shepherdia canadensis* (L.) Nutt.), big willow (*Salix scouleriana* Barr. ex Hook.), and juniper (*Juniperus communis* L.). Ground vegetation was dominated by forbs (*Cornus canadensis* L., *Hedysarum sulphurescens* Rydb., *Lathyrus ochroleucus* Hook., *Aster conspicuus* Lindl., *Epilobium angustifolium* L.), and grasses (*Calamagrostis rubescens* Buckl., *Elymus innovatus* Beal). The forest floor was approximately 6 cm thick, with substantial amounts of incorporated charred wood and large amounts of uncharred wood on the surface. This stand probably originated after a severe fire destroyed a similar stand in 1889 (Johnson 1987, see footnote 1).

The spruce stand was located on a north-facing 3° slope at 1500 m elevation. The soil was an Orthic Dystric Brunisol on an alluvial outwash fan overlying lake deposits (Stalker 1973). The overstory was composed of spruce and pine up to 120 years of age. Canopy trees averaged 20 m in height and had a density of 750 stems/ha and a basal area of 39 $m^2$/ha. Spruce was also predominant in the understory, along with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), aspen, and balsam poplar (*Populus balsamifera* L.). This stand was considerably less dense than the pine stand, with relatively few standing dead or fallen trees. Buffalo-berry and green alder (*Alnus crispa* (Ait.) Pursh) were common shrubs. Ground vegetation was composed of mosses (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G., twinflower (*Linnaea borealis* L.), and forbs (*A. conspicuus*, *E. angustifolium*, *Arnica cordifolia* Hook., *Mertensia paniculata* (Ait.) G. Don). The forest floor was about 12 cm thick, with many large, partially charred boles incorporated. It appears that this stand originated from a similar stand after a fire in 1865 (Johnson 1987, see footnote 1).

The fir site was situated at 1830 m on a 30° slope facing west-northwest. The soil was an Orthic Eutric Brunisol on a layer of glacial till overlying bedrock (Stalker 1973). The overstory was com-

posed of subalpine fir up to 200 years old and spruce up to 350 years old. The height of canopy trees ranged from 15 to 25 m. Density was 1177 stems/ha; stand basal area was 40 $m^2$/ha. As the overstory. Large numbers of dead and fallen trees of both species were present. The shrub layer was dominated by green alder, while mosses (*H. splendens*, *P. schreberi*) dominated the ground vegetation. The forest floor was 12 cm thick on average, with much surface and incorporated wood, none of which was charred. It appears that this forest had not experienced a fire for at least three centuries.

The fourth site (clearcut) was situated in a 1500-$m^2$ area cut from a lodgepole pine forest at 1410 m. The soil was an Orthic Eutric Brunisol on glaciofluvial and fluvial deposits. Live trees had been felled and removed and standing dead trees felled and left on the surface in 1972. Understory trees were left intact and no further site treatment occurred. At the time of survey (1985), the stand was composed of lodgepole pine from 1 to 11 years of age, spruce from 3 to 19 years, willow, aspen, buffalo-berry, and alder. Ground vegetation was composed primarily of grasses (*E. innovatus*, *C. rubescens*), dwarf shrubs (*Arctostaphylos uva-ursi* (L.), *L. borealis*), and forbs (*A. conspicuus*, *E. augustifolium*, *L. ochroleucus*, *C. canadensis*). The forest floor averaged 4 cm deep, with small amounts of incorporated charred wood. Analysis of the surrounding pine forest suggests that this forest is of similar origin to the pine site.

## Methods

*Aboveground biomass and net primary production*

*Trees*

The species and diameter at breast height (DBH) of all live and standing dead trees on two 20 × 30 m plots at each site were recorded in the summer of 1984. Published equations (Singh 1982) were used to convert DBH to aboveground live wood biomass for overstory trees of each species. Published values for the proportion of wood to "foliage" (the current year's and all the previous year's foliage plus current-year twigs) for each species (Keays 1971) were used to calculate the biomass of foliage for each tree. The mass of current-year foliage was estimated as the mass of foliage of each species in annual litter fall. This assumes constant rates of annual litter fall and no consumption losses. Litter fall was harvested monthly from fifteen 0.25-$m^2$ litter traps randomly placed within one 20 × 30 m plot at each site (Prescott *et al.* 1989). The average proportion of total foliage mass that occurred as twigs or as current or previous year's needles was determined for one branch from each of six canopy trees of each species. Foliage production by deciduous trees was estimated using regression equations for each species (Keays 1971).

Annual wood increment of trees was estimated from cores taken from two trees of each 5 cm diameter class of each species at each site. The mass of annual wood increment was determined using regression equations for each species and diameter class and used to estimate the mass of the average annual wood increment of each tree.

Aboveground net primary production (NPP) was calculated as the sum of the biomasses of the current year's needles, the current year's twigs, and annual wood increment for each tree. Total aboveground biomass was calculated as the sum of annual production plus the previous year's needles and wood for each tree. Values were summed for all trees in the 1200-$m^2$ sampling area to estimate NPP and biomass at each site.

Separate DBH–biomass regression equations were derived for understory trees (DBH $<10$ cm) of each species: 10–15 trees of the dominant species (pine, spruce, and subalpine fir) and 4–10 trees of other species (aspen, poplar, and Douglas-fir). Trees were harvested in October 1985 and separated into current year's needles or leaves, current year's twigs, previous year's needles, live wood, and attached dead wood. The average width of annual rings over the last 10 years was again used to determine the mass of new wood. Production and biomass values for individual trees were in other Rocky Mountain spruce–fir forests (Day 1972; Veblen 1986), subalpine fir trees were most numerous in the understory while spruce made up the greatest proportion of the biomass of summed for each species and for all trees on the 1200-$m^2$ sample area to estimate annual NPP and biomass of understory trees at each site. The mass of standing dead trees was estimated using the regressions for live trees minus the mass of foliage.

*Shrubs*

Regression equations relating basal diameter to mass of each biomass component were also developed for each species of shrub. The basal diameter and species of each live stem on three 20 × 30 m plots at each site was recorded in July 1984. For each species (depending on their abundance at the site) 4–15 individual stems across the range of basal diameters present at each site were clipped at ground level and separated into biomass categories. The masses of appropriate components were summed to estimate NPP and biomass of each stem; these were then summed for the sample area (1800 $m^2$) to determine the annual aboveground production and biomass of shrubs at each site.

*Ground vegetation*

Aboveground net primary production and biomass of ground vegetation (grasses, forbs, and small shrubs) were estimated by clipping aboveground portions in ten 0.25-$m^2$ quadrats within one 20 × 30 m plot in August 1985. Harvesting of quadrats at monthly intervals during summer 1984, as well as the results of previous studies in the area (Dennis 1970), indicated early August to be the time of maximum biomass of all species of ground vegetation combined. For herbaceous species, the aboveground mass at peak growth served as the estimate of both NPP and biomass. For woody species, the current year's growth was separated from that of the previous year to calculate annual NPP, and combined to determine total biomass. All live (green) moss was removed from forty 625-$cm^2$ samples of forest floor taken in August 1984 and separated into the current year's and all the previous year's growth. Annual NPP and biomass of each type of ground vegetation (grasses, forbs, small shrubs, and moss) were determined separately.

All samples of vegetation were dried at 80°C before weighing. Samples of each biomass component from six canopy trees, five understory trees, and three shrubs of each species, and five samples of each type of ground vegetation at each site, were analyzed for nitrogen and phosphorus concentrations using a Technicon II autoanalyzer (Technicon Instruments 1976, 1977) following digestion in sulphuric acid and hydrogen peroxide (Lowther 1980). The average N and P contents of each biomass component were multiplied by the mass of that component for each species of tree or shrub or type of ground vegetation, and summed to estimate the total mass of N and P in annual aboveground NPP and biomass.

*Reabsorption of N and P*

The amount of N and P reabsorbed annually by vegetation was calculated from differences in N and P concentrations of green foliage (excluding that of the current year) and senescent foliage. Senescent foliage of each species of tree and shrub and each type of ground vegetation (except moss) was collected in October 1986. Concentrations of N and P in green and senescent foliage were multiplied by the mass of foliage of each species of tree or shrub in annual litter fall or the mass of each type of ground vegetation in annual production to determine the masses of N and P in green and senescent foliage of each species or type of vegetation at each time. The difference in total mass of each nutrient in green and senescent foliage was used as an estimate of the amounts of N and P reabsorbed from foliage annually. This calculation assumes no mass loss or leaching during senescence, and no reabsorption from nonfoliar components.

*Nutrient uptake and nutrient-use efficiency*

Amounts of N and P reabsorbed from foliage annually were subtracted from the amounts in net primary production to estimate the amounts of N and P taken up annually by vegetation to produce

TABLE 2. Masses of N and P in annual net primary production and biomass of aboveground vegetation in four Rocky Mountain coniferous forests

| Site and layer | Net primary production | | | Biomass | | |
|---|---|---|---|---|---|---|
| | Dry mass | N | P | Dry mass | N | P |
| Clearcut | | | | | | |
| Canopy | 0 | 0 | 0 | 0 | 0 | 0 |
| Shrub | 0.62 | 10.24 | 0.88 | 2.93 | 27.44 | 2.43 |
| Ground | 0.74 | 10.17 | 1.56 | 1.17 | 18.00 | 2.37 |
| Total | 1.36 | 20.41 | 2.45 | 4.10 | 45.45 | 4.80 |
| Pine | | | | | | |
| Canopy | 4.57 | 18.96 | 2.65 | 107.41 | 131.03 | 16.11 |
| Shrub | 0.16 | 2.09 | 0.22 | 1.20 | 8.47 | 0.92 |
| Ground | 0.61 | 11.62 | 1.49 | 0.82 | 17.18 | 2.12 |
| Total | 5.34 | 32.68 | 4.36 | 109.43 | 156.58 | 19.14 |
| Spruce | | | | | | |
| Canopy | 4.32 | 17.87 | 2.97 | 198.13 | 263.27 | 29.59 |
| Shrub | 0.35 | 3.70 | 0.56 | 4.02 | 24.40 | 3.99 |
| Ground | 0.47 | 7.36 | 1.44 | 1.05 | 17.29 | 3.23 |
| Total | 5.15 | 28.93 | 4.97 | 203.20 | 304.97 | 36.81 |
| Fir | | | | | | |
| Canopy | 3.83 | 15.98 | 1.92 | 144.07 | 244.78 | 23.75 |
| Shrub | 0.34 | 4.35 | 0.38 | 7.76 | 40.15 | 4.73 |
| Ground | 0.21 | 3.06 | 0.31 | 0.53 | 6.32 | 0.80 |
| Total | 4.37 | 23.39 | 2.61 | 152.36 | 291.25 | 29.28 |

NOTE: Dry mass is given in tonnes per hectare and N and P contents in kilograms per hectare.

TABLE 3. Average N and P concentrations in the major types of ground vegetation in four Rocky Mountain coniferous forests

| Vegetation type* | Site | *n* | % N | % P |
|---|---|---|---|---|
| Moss | Clearcut | 4 | 1.37 ± 0.16*a* | 0.24 ± 0.04*a* |
| | Pine | 5 | 1.49 ± 0.12*a* | 0.25 ± 0.02*a* |
| | Spruce | 5 | 1.18 ± 0.09*a* | 0.24 ± 0.01*a* |
| | Fir | 5 | 1.29 ± 0.32*a* | 0.15 ± 0.04*b* |
| Grasses | Clearcut | 2 | 1.26 ± 0.10*a* | 0.21 ± 0.01*bc* |
| | Pine | 3 | 1.74 ± 0.03*a* | 0.29 ± 0.10*ab* |
| | Spruce | 3 | 1.99 ± 0.18*a* | 0.40 ± 0.03*a* |
| | Fir | 3 | 2.77 ± 0.96*a* | 0.16 ± 0.04*c* |
| Forbs | Clearcut | 2 | 1.81 ± 0.07*a* | 0.20 ± 0.01*b* |
| | Pine | 3 | 2.19 ± 0.27*a* | 0.26 ± 0.05*b* |
| | Spruce | 3 | 1.94 ± 0.17*a* | 0.44 ± 0.05*a* |
| | Fir | 3 | 2.04 ± 0.37*a* | 0.16 ± 0.06*b* |
| Small shrubs (foliage only) | Clearcut | 2 | 1.02 ± 0.01*b* | 0.12 ± 0.00*c* |
| | Pine | 3 | 1.44 ± 0.17*a* | 0.16 ± 0.01*b* |
| | Spruce | 3 | 1.71 ± 0.10*a* | 0.28 ± 0.02*a* |
| | Fir | 3 | 1.79 ± 0.12*a* | 0.10 ± 0.01*c* |

NOTE: Each value is the mean ± standard deviation. For each vegetation type, values in the same column followed by the same letter(s) are not significantly different ($p < 0.05$), based on one-way analysis of variance and Scheffé's test.

*Samples of all species within a quadrat were combined for each vegetation type.

new aboveground biomass. This value was used as a relative estimate of annual uptake or nutrient demand of the vegetation at each site. The efficiency of nutrient use of vegetation at each site was estimated by dividing the amount of new aboveground biomass by the amounts of N and P taken up in 1 year. Additional details on methods used to determine biomass and nutrient concentrations are provided by Prescott (1988).

TABLE 4. Average concentrations of N and P in needles of lodgepole pine and white × Engelmann spruce hybrids at different sites in the Rocky Mountains of southwestern Alberta

| Type | Site | *n* | % N | % P |
|---|---|---|---|---|
| Lodgepole pine needles | | | | |
| Current year | Pine | 6 | 0.93 ± 0.04*a* | 0.13 ± 0.01*a* |
| | Spruce | 6 | 0.94 ± 0.08*a* | 0.12 ± 0.01*a* |
| Current year plus previous year | Pine | 6 | 0.89 ± 0.05*b* | 0.12 ± 0.02*a* |
| | Spruce | 6 | 1.01 ± 0.07*a* | 0.09 ± 0.01*a* |
| White × Engelmann spruce needles | | | | |
| Overstory | | | | |
| Current year | Spruce | 5 | 0.94 ± 0.03*a* | 0.17 ± 0.02*a* |
| | Fir | 5 | 0.93 ± 0.05*a* | 0.12 ± 0.02*b* |
| Current year plus previous year | Spruce | 5 | 0.86 ± 0.04*b* | 0.12 ± 0.01*a* |
| | Fir | 5 | 0.99 ± 0.09*a* | 0.09 ± 0.06*b* |

NOTE: Values are given as mean ± standard deviation. For each type of needle, values within each column followed by the same letter are not significantly different ($p \leq 0.05$) based on *t*-tests for two-mean comparisons or one-way analysis of variance and Scheffé's test for comparisons among four means.

*Statistical analysis*

The significance of differences among sites was tested using one-way analysis of variance followed by Scheffé's test or a *t*-test. Data sets with nonhomogeneous variances according to Bartlett's test were analyzed by the Kruskal–Wallis test. All statistical analyses were carried out using SPSSx (SPSS Inc. 1986).

## Results

The amounts of N and P immobilized in aboveground biomass and NPP in each forest are shown in Table 2. The biomass of aboveground vegetation and the amounts of N and P immobilized therein were highest at the spruce site, followed by the fir, pine, and clearcut sites. This pattern reflects the biomass of the canopy layer at each site. Net primary production and immobilization of N and P therein were highest at the pine and spruce sites. The shrub layer attained its greatest biomass and nutrient mass at the fir site but was most productive at the clearcut site (Table 2). Biomass and production of ground vegetation was greatest at the clearcut site and lowest at the fir site (Table 2). The total amounts of N and P immobilized in aboveground biomass were in the following order: spruce > fir > pine > clearcut; levels of nutrient immobilization in annual production were in the following order: pine > spruce > fir > clearcut.

Concentrations of N and P in each type of ground vegetation at different sites are shown in Table 3. Nitrogen concentrations were similar among sites for all vegetation types, but phosphorus concentrations were consistently lowest at the fir site. Concentrations of P in spruce needles were also lower at the fir site than at the spruce site (Table 4).

The amounts of N and P reabsorbed from aboveground vegetation at each site were closely related to the mass of N in reabsorbing tissue (foliage) present at the site (Fig. 1). Phosphorus reabsorption was less closely related to the mass of P in foliage (Fig. 2), largely as a result of higher P reabsorption by trees and shrubs at the fir site. Exclusion of data from the fir site increased the correlation coefficient

TABLE 5. Concentration and reabsorption of N and P from pine and spruce needles in trees at different sites in the Rocky Mountains of southwestern Alberta

| | | Nitrogen ($mg \cdot g^{-1}$) | | | Phosphorus ($mg \cdot g^{-1}$) | | |
|---|---|---|---|---|---|---|---|
| | Site | Green foliage | Litter fall | Reabsorption* | Green foliage | Litter fall | Reabsorption* |
| Pine | Pine | $8.90 \pm 0.50b$ | $4.61 \pm 0.32a$ | 4.29 (48) | $1.16 \pm 0.18a$ | $0.26 \pm 0.05a$ | 0.90 (78) |
| | Spruce | $10.13 \pm 0.74a$ | $4.48 \pm 0.06a$ | 5.65 (56) | $0.90 \pm 0.11b$ | $0.24 \pm 0.01a$ | 0.66 (73) |
| Spruce | Spruce | $10.56 \pm 1.10a$ | $5.15 \pm 1.04a$ | 5.41 (51) | $1.97 \pm 0.24a$ | $0.61 \pm 0.09a$ | 1.36 (69) |
| | Fir | $10.28 \pm 0.66a$ | $5.37 \pm 0.48a$ | 4.91 (48) | $1.30 \pm 0.18b$ | $0.35 \pm 0.01b$ | 0.95 (73) |

NOTE: Values are given as mean ± standard deviation. For each species, values in different columns followed by the same letter are not significantly ($p \leq 0.05$) different, based on the $t$-test.

*Expressed as concentration of nutrient in green tissue minus concentration of nutrient in litter fall, with percentage of concentration in green tissue shown in parentheses.

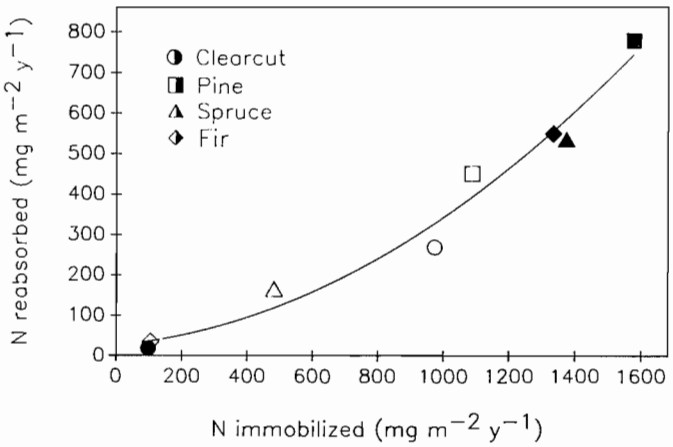


FIG. 1. Relationship between the total mass of N annually incorporated into, and reabsorbed from, foliage in four Rocky Mountain coniferous forests. Open symbols denote ground vegetation and closed symbols denote trees and shrubs ($n = 8$; $y = 2.561 + 0.079x + 0.002x^2$; $r^2 = 0.99$).

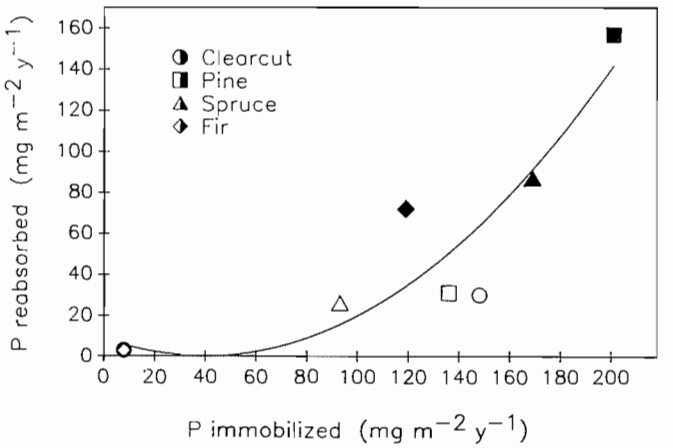


FIG. 2. Relationship between the total mass of P annually incorporated into, and reabsorbed from, foliage in four Rocky Mountain coniferous forests. Open symbols denote ground vegetation and closed symbols denote trees and shrubs ($n = 8$; $y = 8.683 - 0.433x + 0.005x^2$; $r^2 = 0.91$).

($r^2$) to 0.96 from 0.91. The proportions of nutrients present in green tissue that were reabsorbed during senescence were similar in trees of the same species or genus at different sites (Table 5). Trees with greater concentrations of N or P in foliage usually reabsorbed a slightly greater proportion of N or P than those with lower concentrations in live foliage. Spruce needles at the fir site, however, had lower P concentrations and reabsorbed proportionately more P than spruce needles at the spruce site. The amounts of N and P taken up annually by trees and shrubs declined in the following order: spruce > fir > pine > clearcut (Table 6). Nutrient uptake by ground vegetation was greatest at the clearcut site and lowest at the fir site. Uptake of N and P by all aboveground vegetation combined was greatest at the spruce site, followed by the pine, clearcut, and fir sites (Table 6).

Among the mature forests, N was used most efficiently at the pine site and least efficiently at the fir site, while P was used most efficiently at the fir site (Table 6). Although ground vegetation at the clearcut site used both N and P more efficiently than ground vegetation at the other sites, vegetation at the clearcut site was at least efficient overall.

## Discussion

Estimates of net primary production of the mature forests in the Lusk Creek watershed (437–534 $g \cdot m^{-2} \cdot year^{-1}$) were lower than average values of 600 $g \cdot m^{-2} \cdot year^{-1}$ obtained for boreal forests (Lieth 1975) and montane coniferous forests (Olson 1975). This can be attributed to the exclusion of estimates of belowground production in these forests, because the average values for fine root turnover in boreal needle-leaved evergreen forests is 100 $g \cdot m^{-2} \cdot year^{-1}$ (Vogt *et al.* 1986). Aboveground biomass at the pine site was within the range reported for other lodgepole pine forests of similar age and density (Table 7). The N content of the pine stand was similar to that reported in Wyoming but higher than that reported in British Columbia (Table 8). The few spruce–fir stands studied have greater biomass than that at the fir site (Table 7). Biomass and productivity of the forest at the spruce site were about 20% higher than those reported in a white spruce stand (plot 26) of similar age and density in interior Alaska (Yarie and Van Cleve 1983). Nitrogen content of the spruce and fir sites was similar to, and phosphorus content lower than, those reported in a spruce–fir stand in British Columbia (Table 8).

Concentrations of N and P in overstory tree foliage in these forests were similar to those reported in other forests of lodgepole pine (Beaton *et al.* 1965; Kimmins 1974[2]; DeByle 1979; Stark 1983) and Engelmann or white spruce

[2]J.P. Kimmins. 1974. Nutrient removal associated with whole-tree logging on two different sites in the Prince George Forest District. Final Report submitted to British Columbia Forest Service Productivity Committee.

TABLE 6. Annual uptake of N and P and efficiency of use by aboveground vegetation in four Rocky Mountain coniferous forests

| Site | Nitrogen | | | | Phosphorus | | | |
|---|---|---|---|---|---|---|---|---|
| | Annual production[a] | Annual reabsorption[b] | Annual uptake[c] | Efficiency[d] | Annual production[a] | Annual reabsorption[b] | Annual uptake[c] | Efficiency[d] |
| | | | | Tree and shrubs | | | | |
| Clearcut | 1024 | 18 | 1006 | 62 | 89 | 3 | 86 | 721 |
| Pine | 2106 | 777 | 1329 | 357 | 287 | 157 | 130 | 3646 |
| Spruce | 2157 | 534 | 1623 | 288 | 353 | 87 | 266 | 1756 |
| Fir | 2033 | 548 | 1485 | 281 | 230 | 72 | 158 | 2639 |
| | | | | Ground vegetation | | | | |
| Clearcut | 1017 | 269 | 748 | 99 | 156 | 30 | 126 | 587 |
| Pine | 1162 | 450 | 712 | 86 | 149 | 31 | 118 | 517 |
| Spruce | 736 | 165 | 571 | 82 | 144 | 26 | 118 | 398 |
| Fir | 306 | 34 | 272 | 77 | 31 | 3 | 28 | 750 |
| | | | | Total | | | | |
| Clearcut | 2041 | 287 | 1890 | 72 | 244 | 33 | 212 | 642 |
| Pine | 3268 | 1227 | 2041 | 262 | 436 | 188 | 248 | 2157 |
| Spruce | 2893 | 699 | 2194 | 281 | 497 | 113 | 384 | 1604 |
| Fir | 2339 | 582 | 1757 | 249 | 261 | 75 | 186 | 2355 |

NOTE: All data given in milligrams per square metre per year.
[a]Data from Table 4.
[b]Data from Table 7.
[c]Mass of nutrient in annual production minus mass of nutrient reabsorbed annually.
[d]Milligrams of new biomass produced per milligram of N or P taken up in 1 year.

TABLE 7. Aboveground biomass of some Rocky Mountain coniferous forests

| Stand age (yr) | Density (stems/ha) | Biomass ($t \cdot ha^{-1}$) | Location | Source |
|---|---|---|---|---|
| | | | Lodgepole pine | |
| 75 | 1280 | 96.3 | SE Wyoming | Pearson *et al.* 1984 (Rock Creek) |
| 110 | 1850 | 144.1 | SE Wyoming | Pearson *et al.* 1984 (Nash Fork) |
| 71 | 1600 | 70.1 | Central Colorado | Moir 1972 (stand 4.3) |
| 200 | — | 101–104 | Northern Colorado | Reid *et al.* 1976[a] |
| 125 | — | 194.5 | Central British Columbia | Kimmins 1974[b] (Parsnip plot) |
| 100 | 1020 | 245.0 | Southern Alberta | Johnstone 1971 (stand 1) |
| 85 | 1716 | 107.4 | Southern Alberta | This study (pine site) |
| | | | Engelmann or white spruce – subalpine fir | |
| 250 | — | 197.0 | Colorado | Landis and Mogren 1975 (average values) |
| 350 | — | 213.1 | Central British Columbia | Kimmins 1974[b] (McGregor plot) |
| 350 | 1177 | 144.1 | Southern Alberta | This study (fir site) |
| 120 | 750 | 198.1 | Southern Alberta | This study (spruce site) |

[a]C.P.P. Reid, G.J. Odegard, J.C., Hokenstrom, W.J. McConnell, and W.E. Frayer. 1976. Effects of clearcutting on nutrient cycling in lodgepole pine forests. Final report, U.S. For. Serv. grants 16-256-GR and 16-324-6R. Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
[b]J.P. Kimmins. 1974. Nutrient removal associated with whole-tree logging on two different sites in the Prince George Forest District. Final Report submitted to British Columbia Forest Service Productivity Committee.

(Beaton *et al.* 1965; Kimmins 1974 (see footnote 2); Stark 1983, Ballard and Carter 1985). Subalpine fir foliage in the Lusk Creek watershed had higher levels of N and lower levels of P than those found in British Columbia (Kimmins 1974, see footnote 2) and Montana (Stark 1983). Levels of N and P in foliage of pine and spruce were lower than is generally considered adequate for these species (Morrison 1974; van den Driessche 1974; Ballard and Carter 1985). Similar data for subalpine fir are not available. Proportional reabsorption of N from pine needles at these sites (50%) was similar to, and reabsorption of P (75%) was higher than, levels reported for other species of pine (Grizzard *et al.* 1976, cited in Chapin and Kedrowski 1983, Wells and Metz 1963, cited in van den Driessche 1984). Annual uptake of N and P in these forests 18–20 $kg \cdot ha^{-1} \cdot year^{-1}$) was very close to that predicted by Miller (1984) for temperate forests with these rates of net primary production.

Comparison of N and P use by vegetation among the

TABLE 8. Masses of N and P in aboveground biomass of some Rocky Mountain coniferous forests

| Biomass ($t \cdot ha^{-1}$) | N ($kg \cdot ha^{-1}$) | P ($kg \cdot ha^{-1}$) | Source |
|---|---|---|---|
| | Lodgepole pine | | |
| 144.1 | 185 (0.13) | — | Fahey *et al.* 1985 (Nash Fork) |
| 142.2 | 169 (0.12) | — | Fahey *et al.* 1985 (Dry Park 1) |
| 194.5 | 155 (0.08) | 19.8 (0.010) | Kimmins 1974[a] (Parsnip plot) |
| 107.4 | 131 (0.12) | 16.1 (0.015) | This study (pine site) |
| | Engelmann or white spruce – subalpine fir | | |
| 213.1 | 324 (0.15) | 41.7 (0.019) | Kimmins 1974[a] (McGregor plot) |
| 144.1 | 245 (0.17) | 23.7 (0.016) | This study (fir site) |
| 198.1 | 263 (0.13) | 29.6 (0.015) | This study (spruce site) |

NOTE: Numbers in parentheses are percentages.

[a] J.P. Kimmins. 1974. Nutrient removal associated with whole-tree logging on two different sites in the Prince George Forest District. Final Report submitted to British Columbia Forest Service Productivity Committee.

forests examined in the present study allows comment to be made on factors determining patterns of NUE of forests. The low NUE of vegetation at the clearcut site reflects the predominance of shrubs and ground vegetation with higher levels of nutrients in foliage and a more limited nutrient reabsorption capacity than trees. As a consequence, rates of N and P uptake in the young stand at the clearcut site are similar to those in the mature forests. This emphasizes the ability of fast-growing early successional vegetation to retain nutrients within recently disturbed ecosystems (Marks and Bormann 1972; Vitousek and Reiners 1975).

The low levels of N and P in annual production, biomass, and foliage, and greater N and P reabsorption at the pine site, demonstrate efficient nutrient use by trees at this site. Lodgepole pine trees at both the pine and spruce sites used N and P efficiently, as was found in other lodgepole pine forests, which suggests that this efficiency is a characteristic of pine trees and not an indication of low nutrient availability at the pine site. High efficiency of water and nutrient use has been demonstrated for other species of pines (Miller *et al.* 1979); thus, the prevalence of this species is probably responsible for the efficient use of N and P by vegetation at the pine site.

Reabsorption of N and P by overstory trees at the spruce site was relatively low, resulting in high rates of N and P uptake and low efficiency of use of these nutrients at this site. The amounts of N and P in tree biomass and annual production (requirement) and the efficiency of use of both nutrients at the spruce site are similar to average values for white spruce stands in interior Alaska (Van Cleve *et al.* 1983). Concentrations of N and P in foliage and efficiency of reabsorption of N and P from foliage of pine and spruce trees at this site were similar to values for the same species at the other sites and in other forests, suggesting that the relatively low efficiency of N and P use by this stand is a consequence of the predominance of nutrient-inefficient spruce trees in this forest.

Nitrogen concentrations in vegetation at the fir site were similar to those at the spruce site and other spruce–fir forests (Kimmins 1974, see footnote 2), as was the degree of N reabsorption and the efficiency of N use. Phosphorus concentrations were lower in all types of vegetation at the fir site than at the other sites and in other forests, and P was used much more efficiently by vegetation at this site. Levels of extractable P in the forest floor are consistently lower at the fir site than at the other sites (Prescott 1988), suggesting that low availability of P has led to greater P-use efficiency in this forest.

It appears that differences in N- and P-use efficiency among the three mature stands are mostly due to differences in species composition of the overstory. Patterns of species composition in these forests are the result of the interplay of many factors, such as disturbance regime and microclimate, in addition to nutrient availability. Therefore, it is unlikely that the observed differences in species composition (and hence NUE) of these stands reflect differences in availability of N and P among the sites. An overriding influence of species composition, regardless of nutrient availability, on mineral nutrition of whole stands has been implicated in the fertilization experiments of Shaver and Lechowicz (1985). Although rates of N and P mineralization in the forest floor were related to NUE of the stands (Prescott 1988), this is more likely a consequence of the N and P content of litter produced by vegetation in each forest than a determinant of species composition and NUE of the forests. Experiments currently in progress to measure the N- and P-supplying power of mineral soil from each site will elucidate the relationship between inherent fertility of the soil and species composition – NUE of vegetation in these forests. Finally, there is some evidence of greater NUE by vegetation on infertile sites, unrelated to changes in species composition, in the greater efficiency of P use by all types of vegetation at the fir site.

Comparison of the amounts and proportions of N and P reabsorbed by vegetation at each site lends insight into the relative importance of this mechanism compared with greater biomass production per unit nutrient uptake in determining NUE of vegetation in these forests. The positive relationship found in most situations between the total mass or concentration of N and P in foliage and the amount and proportion of N and P reabsorbed is consistent with the findings of Lajtha (1987) for *Larrea tridentata* (DC.) Cov. This suggests that the amounts and proportions of N and P reabsorbed depend primarily on the amounts available in foliage for reabsorption. The occurrence of the opposing trend of slightly greater reabsorption efficiency of P at low P concentrations in foliage at the fir site suggests that where availability of a nutrient is particularly low, a slightly greater proportion (but a lower total amount) of the nutrient may be reabsorbed.

The small differences in reabsorption efficiency relative to the differences in nutrient content of vegetation among species and sites suggest that production of greater biomass per unit N or P uptake is the major mechanism of NUE in these forests. A similar conclusion was reached by Birk and Vitousek (1986) with respect to N-use efficiency of *Pinus taeda* L.

Analysis of the nutrient content of foliage or litter fall has often been suggested as a simple and reliable means of assessing nutrient availability or deficiency in forests

(van den Driessche 1974; Waring and Schlesinger 1985). The reliability of this technique requires demonstration that nutrient concentrations in foliage from sites with different nutrient availability are detectably different from one another. The limited data presented in the study suggest that these species of trees are remarkably consistent in their levels of nutrients in foliage, regardless of location. However, it appears that substantial differences in nutrient availability (as suggested for P at the fir site) may be detected through analysis of the nutrient content of foliage or litter fall.

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